HortScience 42(6):1440–1449. 2007.

Seasonal Variation in Growth, Nitrogen Uptake and Allocation by Container-grown Evergreen and Deciduous Rhododendron Cultivars

Carolyn F. Scagel[1]
U.S. Department of Agriculture, Agricultural Research Service, Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, OR, 97330

Guihong Bi[2] **and Leslie H. Fuchigami**
Department of Horticulture, Oregon State University, Corvallis, OR

Richard P. Regan
Department of Horticulture, North Willamette Research and Extension Center, Oregon State University, Aurora, OR

Additional index words. Rhododendron 'English Roseum', Rhododendron 'P. J. Mezitt Compact', Rhododendron 'Gibraltar', azalea, nitrogen use efficiency

Abstract. **Growth, nitrogen (N) uptake, and N storage were assessed in transplanted 1-year-old rhododendron liners. Two evergreen cultivars, *Rhododendron* 'P. J. Mezitt Compact' (PJM) and R. 'English Roseum' (ER), and one deciduous cultivar, R. 'Gibraltar' (AZ), were transplanted into 1-gal. pots and given liquid fertilizer with (+N) or without (–N) N. Increased N availability increased growth after July (ER, PJM) or August (AZ), and resulted in three to five times more total biomass. Biomass continued to increase after stem elongation and leaf production ceased. Nitrogen uptake was correlated with growth of all plant structures on AZ, whereas N uptake was only correlated with stem and leaf growth on evergreen cultivars. The rate of N uptake was highest before July for AZ (1.9 mg·d^{-1}) and in August and September for the evergreen cultivars (≈5 mg·d^{-1}). Thirteen percent to 16% of total N uptake from between May and February occurred after N fertilization ceased at the beginning of September. Plants contained the most N in October (AZ), November (PJM), or December (ER). Biomass loss after November accounted for a loss of 14% to 48% of the maximum total plant N content. Nitrogen demand by roots and stems increased from May to February in all cultivars. The role of new and old leaves in N storage on evergreen cultivars varied with cultivar and time. Differences in N storage between the evergreen cultivars occurred primarily in their roots and leaves. Over the winter, PJM stored more N in its roots, whereas ER stored more N in its leaves. Changes in N concentrations and contents in different plant structures after November indicate that, during early winter, N stored in other structures moves to roots and old stems of PJM, old stems of ER, and roots and new and old stems of AZ. These results suggest that fertilizer application strategies for transplanted liners of these cultivars should include low N availability after transplanting followed by high N availability in mid to late summer. This type of strategy will not only improve N uptake efficiency from fertilizer, but also will minimize N loss from the containers. The results also demonstrated that N uptake in the autumn may play an important role in supplementing plant N reserves required for growth during the next season as well as for balancing N losses incited by leaf abscission, root turnover, and maintenance functions that occur over winter.**

Improved fertilization guidelines and more effective fertilizers need to be designed to optimize nutrient use efficiency and to minimize leaching in production of container-grown nursery plants. Container-grown plants are often fertilized with controlled-released fertilizers (CRFs). Depending on crop nutrient demands and production temperatures, nutrient release from these fertilizers are sometimes excessive during the first half of an annual production cycle and insufficient during later stages of production (Broschat, 2005; Huett and Gogel, 2000; Merhaut et al., 2006). Therefore, CRFs can be quite inefficient when release patterns do not match plant requirements, which often vary with both cultivar and environmental conditions (Cabrera, 1997). To improve fertilizer formulations and schedules for nurseries, more information on fertilizer use and fertilizer uptake efficiency is needed (Sandrock et al., 2005a).

Rhododendron (Ericaceae) is grown in many nurseries in the United States. Many growers transplant 1-year-old liners into larger containers during April and May to produce 2-year plants for retail. Controlled-release fertilizers containing high amounts of nitrogen (N) are often applied during transplanting, and plants are commonly given liquid fertilizer supplements during the growing season. Nitrogen requirements of *Rhododendron* species are fairly well studied in natural environments (Jonasson, 1995; Karlsson, 1994a, b; Lamaze et al., 2003; Pasche et al., 2002a, b), but little is known about requirements under nursery conditions (Witt, 1994). Recently, Bi et al. (2006) assessed N uptake and partitioning in two different cultivars of *Rhododendron* from May through September. They determined that although N uptake occurred throughout the experiment, adding more N to the growing substrate had no effect on plant growth until July. They also found that N uptake efficiency varied between *Rhododendron* cultivars and that timing of demand differed among plant structures.

In other ericaceous species, growth and nutrient uptake have been observed in the autumn and early winter when environmental conditions are conducive for root activity (Andersen and Michelsen, 2005; Grelet et al., 2001). Plant N status at the end of the growing season is positively correlated with plant growth in the following spring for many plant species (Millard, 1996); however, the contribution of potential autumn and winter nutrient uptake to N status in container-grown *Rhododendron* has not been investigated. The objective of the current study was to expand our knowledge of N uptake and allocation by container-grown *Rhododendron* by characterizing the plant growth, the extent of N uptake, and the changes in N storage that occur during the autumn and winter. Information about autumn and winter N uptake by evergreen and deciduous *Rhododendron* cultivars will help nursery growers and fertilizer manufacturers develop more efficient fertilization strategies.

Received for publication 2 Feb. 2007. Accepted for publication 29 Mar. 2007.
This work was funded, in part, by the USDA-ARS, Northwest Center for Nursery Crop Research and the Oregon State Agricultural Research Foundation.
We gratefully acknowledge the technical assistance of Jesse Mitchell, Ben Ervin, Summer Hendricks, Kevin Mitchell, Maryann Resendes, and Sueann Ott. We also thank Drs. David Bryla and James Owen for their constructive comments on an earlier version of this manuscript, and Brigg's Nursery, Olympia, Washington, for plant material.
Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products or vendors that also my be suitable.
[1]To whom reprint requests should be addressed; e-mail scagelc@onid.orst.edu
[2]Current address: Department of Plant and Soil Sciences, Truck Crops Branch Experiment Station, Mississippi State University, 2024 Experiment Station Road, Crystal Springs, MS.

Materials and Methods

Plant culture and treatments. One-year-old liners of two evergreen cultivars of *Rhododendron*, 'P.J.M. Compact' (PJM) and 'English Roseum' (ER), and one deciduous cultivar, 'Gibraltar' (AZ), were transplanted on 25 Apr. 2005 into black, 3.8-L (1-gal.) containers (GL-400; Nursery Supplies, McMinnville, OR) filled with a substrate of bark, sphagnum peatmoss, perlite, vermiculite, dolomitic lime, gypsum, and a proprietary wetting agent (SB-300; Sun Gro Horticulture, Bellevue, WA). Plants were grown outdoors in Corvallis, OR (45°59′04″ N, 123°27′22″W). Forty plants from each cultivar were randomly assigned to one of two groups and fertilized twice a week from 29 Apr. to 2 Sept. 2005. During each application, one group (–N treatment) received 250 mL N-free fertilizer (1.06 $mg \cdot mL^{-1}$; Cornell No N Eq. 0-6-27, Greencare Fertilizers, Kankakee, IL) whereas the other (+N treatment) received 250 mL N-free fertilizer plus 140 $mg \cdot L^{-1}$ N (NH_4NO_3; Sigma Aldrich, St. Louis). Plants were watered by drip irrigation to container capacity twice a day (8:00 AM and 3:30 PM) from 2 May to 30 Sept. 2005 using one drip emitter (2 $L \cdot h^{-1}$ flow rate; Netafim Co., Valley Stream, NY) per container. The N concentration in irrigation water was measured periodically from May to October using ion selective electrodes (Thermo Electron Corp., Waltham, MA). Concentrations of nitrate and ammonium in irrigation water were less than 28 $mg \cdot L^{-1}$ NO_3 and 10 $mg \cdot L^{-1}$ NH_4. The N supplied from irrigation water was accounted for in total N uptake estimates. The irrigation requirements were corrected weekly based on gravimetric determination of container capacity measured in +N reference plants of each cultivar. Weather data including temperature, precipitation, and reference evapotranspiration were obtained for the duration of the experiment from a U.S. Bureau of Reclamation AgriMet weather station (CRVO) located ≈5 km from the experimental site.

Measurements. Five plants from each treatment were randomly selected and harvested at transplanting and about every 4 weeks from 18 July 2005 to 1 Feb. 2006. Stems were cut at the soil surface and separated into leaf and stem components. Leaves were counted and total leaf area was estimated using an LI-3000 area meter (LI-COR Environmental, Lincoln, NE). Stem length was also recorded. When applicable, stems and leaves were divided into 1-year-old and 2-year-old structures. Roots were removed from the containers and washed from the substrate. Leaves, stems, and roots were oven dried to a constant weight at 65 °C, weighed, ground (60 mesh), and analyzed for carbon (C) and N concentrations using a CN combustion analyzer (Tru Spec CHN; LECO Corporation, St. Joseph, MI).

Calculations. Relative growth rate ($mg \cdot g^{-1} \cdot d^{-1}$) was calculated as described in Hoffman and Poorter (2002) by calculating the average change in biomass of the different plant structures between harvest dates [e.g., $(\ln W_x - \ln W_{x-1})/(T_x - T_{x-1})$; where W_x is biomass at harvest T_x and W_{x-1} is the average biomass within a treatment at harvest T_{x-1}]. Leaf, stem, and root C and N content (measured in milligrams) was calculated by multiplying C and N concentration from samples of each structure by the dry weight of each structure. Total C and N content (measured in milligrams) was calculated as the sum overall structures. Nitrogen uptake (measured in milligrams per day) was calculated as the difference in total N content between harvests whereas N uptake from fertilizer (measured in milligrams) was calculated as the difference between average N uptake by +N and –N plants. Efficiency of N uptake from fertilizer (as a percentage) was estimated by dividing N uptake from fertilizer by +N plants by the total amount N applied to the plants as fertilizer. The amount of N in each plant structure was used to characterize N use and storage at each harvest date. Changes in N content in each structure of +N plants, expressed as the percentage of total cumulative N uptake, were used to determine the times of N demand (use and storage) (Marschner, 1995; Milla et al., 2005).

Use of ^{15}N is considered an accurate and sensitive method to determine fertilizer N uptake and uptake efficiency (Chapin and van Cleve, 1991; Proe et al., 2000), although this method sometimes 1) underestimates uptake when ^{15}N is immobilized by substrate components and nonlabeled substrate N is released (Sandrock et al., 2005b; Walters and Malzer, 1990), and 2) overestimates storage and demand as a result of preferential N pool substitution within the plant (Kolb and Evans, 2002). This method can be cost prohibitive, especially when analyzing the large number of samples required to assess seasonal uptake in perennial plants. Using a total N method (sensu Sandrock et al., 2005b) also has inherent limitations. For example, this method does not account for uptake from soilless substrate or irrigation water. Furthermore, the method underestimates remobilization when using changes in pool size from sequential samples (Jonasson, 1989; Proe et al., 2000), and does not clearly differentiate between internal remobilization and root uptake (Proe et al., 2000). In our study we estimated background N uptake from nonfertilizer sources by growing plants without additional N amendment from fertilizer. Although this estimate may be biased by size differences between +N and –N plants, and the effects of +N on mineralization, availability, and uptake of substrate N (Azam et al., 1989), we suspect that our corrected estimates of total N uptake provides more reasonable approximations of N uptake than simply ignoring potentially significant contributions of nonfertilizer N sources. Sandrock et al. (2005b) found that differences in N uptake efficiency estimates between the ^{15}N fertilizer and total N methods were larger at low rates of fertilizer application than at high rates. In our prior work on *Rhododendron* (Bi, unpublished data), we found that N application rates similar to those used in this study were in excess of plant requirements for growth. This suggests that our estimates of N uptake efficiency may be close to those obtained using ^{15}N.

Experimental design and statistical analyses. Containers were arranged in a completely randomized design with two rates of N fertilizer (–N and +N), three cultivars (PJM, ER, and AZ), nine harvest dates, and five replicates per treatment. Data were analyzed using mixed-model analysis of variance (ANOVA) with cultivar, N fertilizer, and harvest date as main effects, and cultivar considered a random effect. Relative growth rate, N uptake, efficiency of N uptake from fertilizer, and change in N content data were transformed before analysis to correct for unequal variance and achieve a best model fit. Changes in each variable over time are presented in tables and graphs using means and SES, after back transformation when appropriate. When indicated by ANOVA, means were separated using Tukey's HSD or Tukey's HSD for unequal N at $P = 0.05$ ($THSD_{0.05}$). Biomass and N accumulation between +N and –N plants within and between cultivars were compared using specific contrasts at $P < 0.05$. Differences in seasonal patterns of biomass and N accumulation and changes in N between cultivars were compared using polynomial contrasts at $P < 0.05$. Relationships between response variables were assessed using Spearman's rank order correlation coefficient (R) at $P < 0.05$. All analyses were performed using the Statistica statistical package (1996, Statsoft, Tulsa, OK).

Results and Discussion

Growth response to nitrogen availability. Increased N availability had little effect on biomass accumulation until after July 2005 for evergreen cultivars (PJM and ER), whereas the response to N was delayed in the deciduous cultivar (AZ) until Aug. 2005 (Fig. 1). In perennial plants, remobilization of internal resources for new growth in the spring is an important mechanism that enables plants to be partly independent of nutrient supply. Lack of dependence on soil N until later in the season has been reported in *R. ferrugineum* and other ericaceous plants (*Vaccinium myrtillus* and *V. vitis idaea*) (Grelet et al., 2003; Lamaze et al., 2003; Pasche et al., 2002a). In *Vaccinium*, soil N availability only altered growth after a second leaf flush and not before. Bi et al. (2006) reported that total biomass of two *Rhododendron* cultivars (P.J.M. H-1 and Cannon's Double) did not depend on fertilizer N until July and that dependence occurred earlier in the faster-growing cultivar ('Cannon's Double'). In the current study, maximum accumulation of biomass was greater in the two evergreen cultivars than in the deciduous cultivar (Fig. 2) and the evergreen cultivars also responded earlier to increased N availability (Fig. 1). The positive correlations we

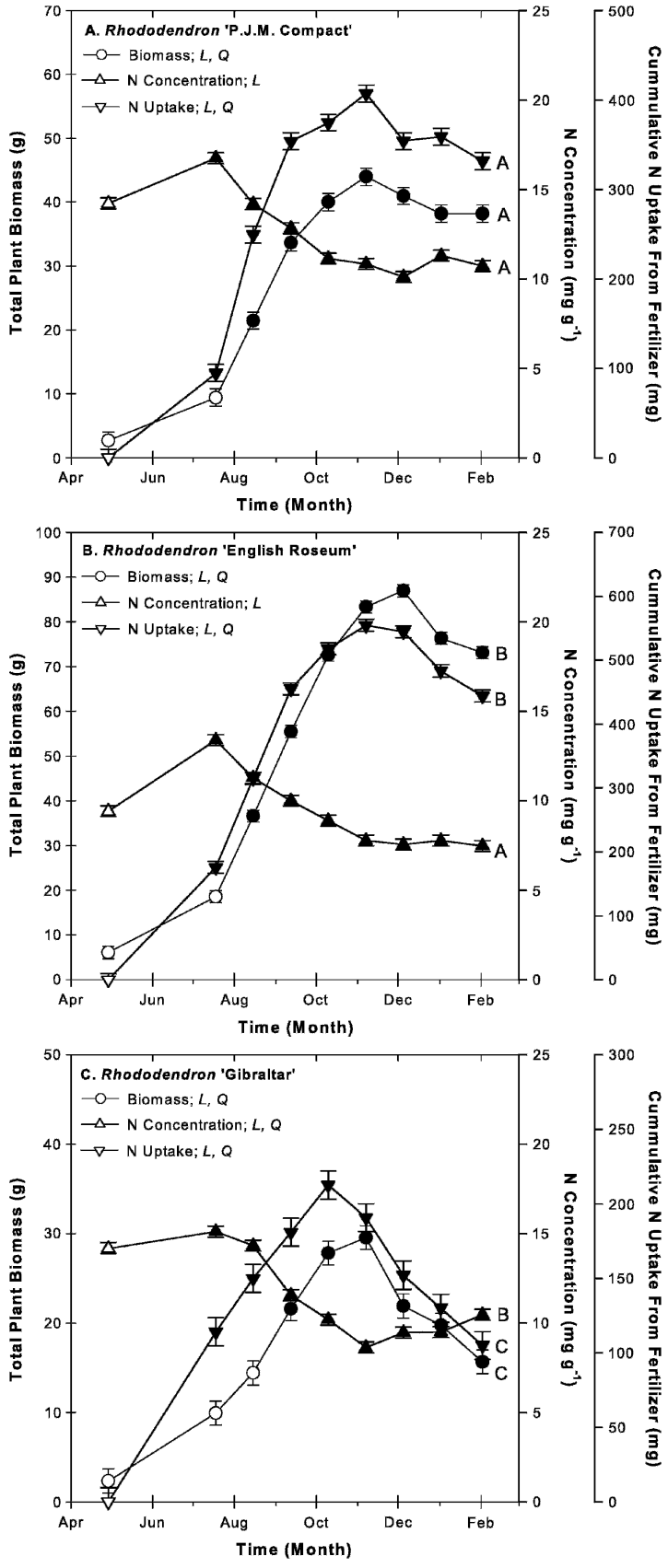

Fig. 1. Total biomass, nitrogen (N) concentration, and cumulative N uptake from fertilizer of three *Rhododendron* cultivars grown in containers with (+N) or without (–N) additional N. Data points represent means; error bars represent SES (n = 5). Solid data points denote means within a response variable and cultivar that are significantly greater than corresponding means for plants in the –N treatment ($THSD_{0.05}$). Uppercase letters to the right of lines denote significant differences within a response variable over time between cultivars (contrasts at $P < 0.05$). The *L* and *Q* in legends after a response variable represent significant ($P < 0.05$) linear (*L*) and quadratic (*Q*) contrasts over time.

observed between total plant growth rate and rate of N uptake (PJM, $R = 0.880$; ER, $R = 0.926$; AZ, $R = 0.904$) also indicate N uptake rate after transplanting is a function of total plant growth rate.

The positive relationship between total plant growth rate and rate of N uptake is predictable; however, application of this concept to developing fertilizer practices is complex. We found that growth, in terms of stem elongation and leaf production, stopped in July (AZ) and in August (PJM, ER), before total biomass accumulation ceased. Neither stem elongation nor leaf production was influenced by N availability (data not shown). Thus, if only stem elongation and leaf production were used to estimate plant nutrient requirements, then estimates obtained would not account for accumulation of biomass that occurred after stem elongation and leaf production ceased. This helps to explain the total asynchrony between shoot N requirements and root N uptake reported for *R. ferrugineum* (Pasche et al., 2002a).

Biomass accumulation of certain plant structures, such as new leaves, responded earlier to increased N availability than other structures, such as old leaves, stems, and roots (Tables 1 and 2). Nitrogen requirements in some woody species change with dry matter accumulation as well as with the stage of plant development (Bi et al., 2006; Sandrock et al., 2005b). In many studies, however, N accumulation is only monitored for 3 to 4 months. Few studies have addressed how changes in biomass and nutrient demands in autumn influence N uptake and use later in the year. Nitrogen demands of different plant structures vary over time. Therefore, understanding long-term seasonal growth patterns of these structures is important for developing complete N fertilizer strategies based on growth.

The growth response of different plant structures to N was not always related to differences in N uptake. For example, N uptake by the deciduous cultivar was positively correlated with growth of all plant structures including roots ($R = 0.816$), new stems ($R = 0.662$), old stems ($R = 0.747$), and leaves ($R = 0.777$), but was not related to growth of all structures in the other two cultivars. Only growth of roots (PJM, $R = 0.811$; ER, $R = 0.773$) and old stems (PJM, $R = 0.667$; ER, $R = 0.653$) were positively correlated with N uptake in evergreen cultivars, suggesting that new stem and leaf growth on these cultivars after May is a function of N uptake and remobilization before May. Our results are important examples of when basing fertilizer recommendations on the rate of plant growth, it is important to know not only how long plant growth was determined, but also how plant growth was estimated.

Seasonal patterns in biomass allocation and root growth. Increasing N availability altered biomass allocation in *Rhododendron* and each cultivar exhibited distinctly different patterns (Fig. 3). Bi et al. (2006) reported that higher rates of N fertilizer application

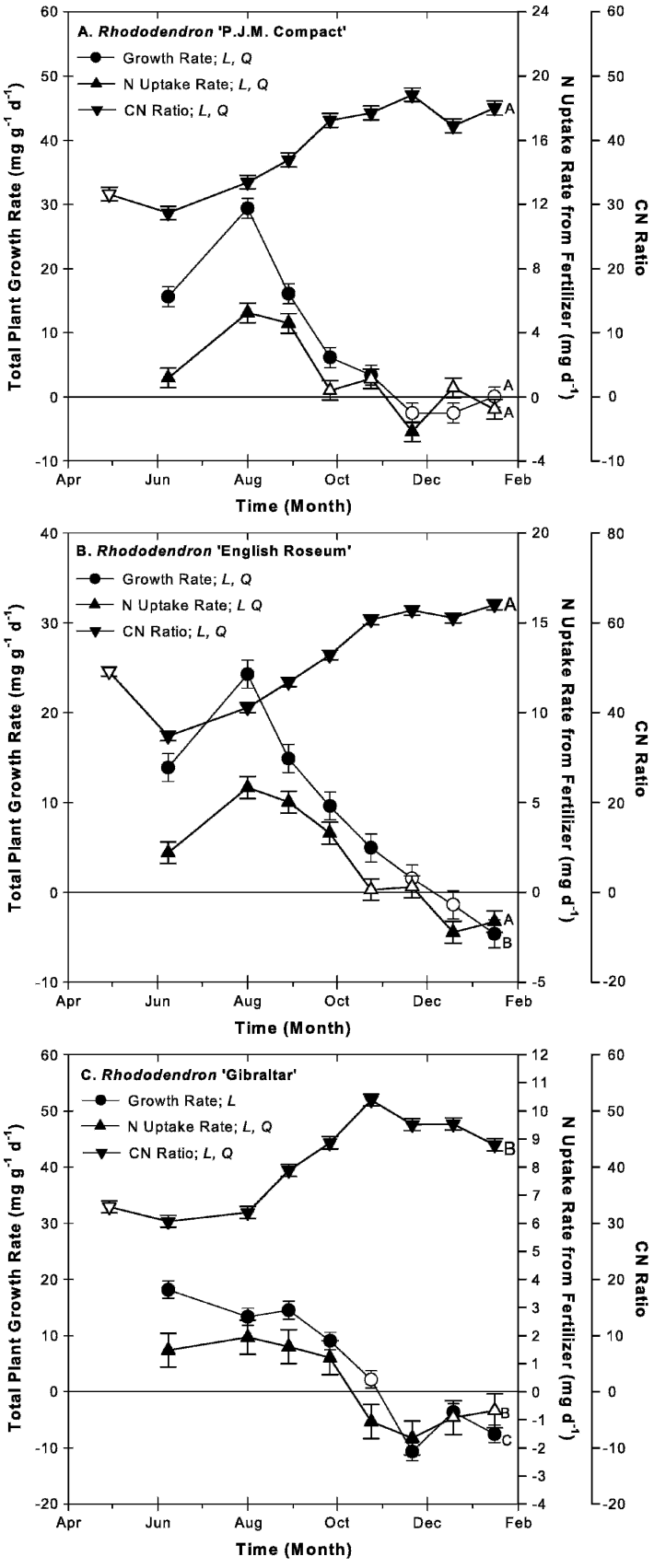

Fig. 2. Total plant growth rate, rate of nitrogen (N) uptake from fertilizer, and carbon-to-nitrogen ratio (CN) of three *Rhododendron* cultivars grown in containers with (+N) or without (–N) additional N. Data points represent means; and error bars represent SES (n = 5). Solid data points denote means within a response variable and cultivar that are significantly greater than corresponding means for plants in the –N treatment ($THSD_{0.05}$). Uppercase letters to the right of lines denote significant differences within a response variable over time between cultivars (contrasts at $P < 0.05$). The *L* and *Q* in legends after a response variable represent significant ($P < 0.05$) linear (*L*) and quadratic (*Q*) contrasts over time.

increased the ratio of aboveground to belowground biomass of container-grown *Rhododendron,* but only in August and only for the ratio of new aboveground biomass to root biomass. Similar results have been reported for other *Rhododendron* cultivars and for other species as a mechanism used by plants to optimize available resources by allocating more resources to the acquisition of nutrients when they limit growth (Alt et al., 1994; Bloom et al., 1985). However, in our current study, allocation also varied among cultivars after August, and even the ratio of old (2004) aboveground biomass to root biomass was affected by N availability in the evergreen cultivars, which suggests that changes in biomass allocation after September may reflect increased storage in aboveground structures.

By February, biomass changes in roots and aboveground structures (Table 1) resulted in N availability having no influence on the ratio of aboveground to root biomass for two of the three cultivars (Fig. 3). This suggests maintaining a balance between root and aboveground biomass may be important for certain *Rhododendron* cultivars. This type of balance may be important for perennial plants in which resource availability can vary greatly between years, and maintaining a balance between resource allocation in aboveground and belowground minimizes the potential of environmental stress. Plants with large shoot-to-root ratios can be more susceptible to transplant shock, moisture, and temperature stress, and may have poor establishment (Andersen and Bentsen, 2003; van den Driessche, 1991).

The seasonal growth patterns of various plant structures varied among cultivars (Table 2). Root growth was always correlated to total plant growth (PJM, $R = 0.861$; ER, $R = 0.877$; AZ, $R = 0.904$), but not necessarily related to stem and leaf growth. For example, root growth was only correlated with growth of old stems ($R = 0.770$) and old leaves ($R = 0.612$) in PJM, new stems ($R = 0.680$) in ER, and old stems ($R = 0.644$) and new leaves ($R = 0.867$) in AZ. There are many reports of opposing shoot and root growth in woody plants (Harris et al., 1995; Mertens and Wright, 1978). Roots on perennial plants generally have the greatest growth in early spring before shoot growth, and in late summer and early autumn after stem elongation. Root growth may also peak before May in *Rhododendron*, but early-season growth was not measured in our study. The positive relationships we found between N uptake and root growth for all cultivars (PJM, $R = 0.811$; ER, $R = 0.823$; AZ, $R = 0.904$) indicate that understanding how production practices influence root growth periodicity may be an important factor in improving nutrient utilization in container production.

Differences among cultivars in root biomass accumulation may not only be related to root system development, but may also be a function of increased storage. For example, root biomass of PJM increased from May to February, and although the rate of biomass

Table 1. Biomass of roots, new (2005) stems and leaves, and old (2004) stems and leaves of *Rhododendron* 'P.J.M. Compact' (PJM), *R.* 'English Roseum' (ER), and *R.* 'Gibraltar' (AZ) grown in containers with (+N) or without (–N) additional nitrogen (N) from Apr. 2005 to Feb. 2006.

		Biomass (g)									
		Roots		2005 Stems		2004 Stems		2005 Leaves		2004 Leaves	
Cultivar	Date	–N	+N	–N	+N	–N	N+	–N	+N	–N	+N
PJM	04/29/05	0.62	0.62	0.06	0.06	0.47	0.47	0.72	0.72	0.81	0.81
	07/18/05	2.19	1.83	0.47	0.81	1.30	1.33	2.28	4.91	0.76	0.54
	08/15/05	3.37	4.17	0.60	3.10*	0.71	1.95	1.83	11.53*	0.45	0.70
	09/12/05	4.53	9.32*[y]	0.74	3.66*	1.72	6.38*	2.46	9.79*	0.43	4.52*
	10/10/05	4.91	11.33*	0.72	4.11*	1.78	10.46*	1.48	9.38	0.68	4.71*
	11/07/05	4.79	14.33*	0.62	4.42*	1.55	11.38*	1.51	8.93*	—	4.92*
	12/05/05	4.77	14.59*	0.76	5.32*	1.20	8.37*	1.37	9.89*	—	2.82*
	01/02/06	4.76	15.37*	0.52	4.72*	1.53	5.46*	1.55	9.77*	—	2.86*
	01/30/06	4.28	16.50*	0.86	4.57*	1.76	5.56*	1.82	11.59	—	—
ER	04/29/05	1.25	1.25	1.48	1.48	0.33	0.33	1.34	1.34	1.68	1.68
	07/18/05	3.82	4.03	0.91	1.86	1.19	1.76	3.09	8.02*	2.31	2.88
	08/15/05	6.10	7.44	1.76	5.44*	1.12	2.01	4.09	19.88*	1.42	1.83
	09/12/05	7.23	11.93*	0.99	7.07*	1.47	7.09*	2.89	21.49*	2.76	7.91*
	10/10/05	9.94	14.25*	1.55	7.22*	2.03	7.55*	4.97	28.23*	2.76	15.35*
	11/07/05	9.38	20.38*	1.19	11.18*	1.33	7.95*	2.98	27.49*	1.24	16.38
	12/05/05	9.27	18.73*	1.46	12.39*	1.61	9.46*	4.46	28.23*	1.78	18.17*
	01/02/06	9.74	18.59*	1.74	11.28*	1.27	8.15*	3.98	28.94*	1.81	9.39*
	01/30/06	7.97	16.56*	1.64	9.67*	1.69	6.43*	4.17	34.47*	1.71	6.00*
AZ	04/29/05	0.98	0.98	0.11	0.11	0.51	0.51	0.73	0.73	—	—
	07/18/05	2.43	3.92	0.34	0.93	0.93	1.38	1.45	3.69	—	—
	08/15/05	5.09	6.02	0.55	1.54	0.88	2.17	1.71	4.66*	—	—
	09/12/05	7.00	8.35	0.71	5.56*	1.67	2.83	1.92	4.85*	—	—
	10/10/05	7.86	13.48*	0.79	4.39*	1.42	3.61*	1.98	6.30*	—	—
	11/07/05	8.76	16.39*	0.79	4.34*	1.19	3.42*	0.46	5.37*	—	—
	12/05/05	8.29	13.50*	0.51	3.41*	0.95	3.17*	—	1.79	—	—
	01/02/06	7.75	13.19*	0.75	3.63*	1.11	2.91*	—	—	—	—
	01/30/06	6.64	10.35*	0.59	2.22*	1.02	3.05*	—	—	—	—
Contrasts[y]											
PJM (time)		L, Q	L, Q	NS	L, Q	NS	L, Q	NS	L, Q	NS	L, Q
ER (time)		L, Q	L, Q	NS	L, Q	NS	L, Q	L	L, Q	NS	L, Q
AZ (time)		L, Q	L, Q	NS	L, Q	NS	L, Q	NS	Q	—	—
PJM vs. ER (time)		L, Q	Q	NS	L, Q	NS	L, Q	L	L, Q	NS	L, Q
PJM vs. AZ (time)		L, Q	L, Q	NS	L, Q	NS	L, Q	NS	L, Q	—	—
ER vs. AZ (time)		NS	L	NS	L	NS	L, Q	L	L, Q	—	—

[z]Asterisks beside +N denote significant differences between +N and –N treatments within a date ($THSD_{0.05}$; n = 5).
[y]Significant ($P < 0.05$) polynomial responses of variables over time for each cultivar and between cultivars.
AZ, *Rhododendron* 'Gibraltar'; ER, *R.* 'English Roseum; L, linear; +N, with nitrogen; –N, without nitrogen; PMJ, *R.* 'P.J.M. Compact' (PJM); Q, quadratic.
[NS]Nonsignificant.

Table 2. Growth rate of roots, new (2005) stems and leaves, and old (2004) stems and leaves of *Rhododendron* 'P.J.M. Compact' (PJM), *R.* 'English Roseum' (ER), and *R.* 'Gibraltar' (AZ) grown in containers with additional nitrogen (N) from Apr. 2005 to Feb. 2006.

		Growth rate ($mg \cdot g^{-1} \cdot d^{-1}$)				
Cultivar	Date	Roots	2005 Stems	2004 Stems	2005 Leaves	2004 Leaves
PJM	04/29/05–07/18/05	13.1*[z]	32.4*	12.4*	23.8*	–5.2
	07/18/05–08/15/05	29.1*	47.2*	13.3*	30.4*	8.3
	08/15/05–09/12/05	28.3*	15.2*	41.8*	–6.8*	63.1*
	09/12/05–10/10/05	6.8*	2.9	17.3*	–2.3	–5.3
	10/10/05–11/07/05	8.2*	2.0	2.4	–2.1	–0.4
	11/07/05–12/05/05	1.5	5.9*	–11.1*	2.7	–20.7*
	12/05/05–01/02/06	1.7	–5.1	–15.8*	–2.3	–3.3
	01/02/06–01/30/06	1.8	–2.0	–0.3	5.4*	–
ER	04/29/05–07/18/05	14.7*	1.1	20.4*	21.7*	5.6
	07/18/05–08/15/05	21.4*	38.1*	3.6	32.4*	–18.1*
	08/15/05–09/12/05	16.6*	9.1*	44.3*	7.6*	51.9*
	09/12/05–10/10/05	6.1*	0.5	1.5	9.4*	23.4*
	10/10/05–11/07/05	12.6*	15.4*	1.7	–1.1	2.1
	11/07/05–12/05/05	–3.1	13.5*	5.9*	0.9	3.3
	12/05/05–01/02/06	–1.4	–13.4*	–5.8*	0.6	–25.2*
	01/02/06–01/30/06	–4.3*	–15.6*	–8.6*	6.1*	–16.3*
AZ	04/29/05–07/18/05	17.1*	25.6*	12.0*	19.6*	—
	07/18/05–08/15/05	14.9*	17.7*	15.1*	8.1*	—
	08/15/05–09/12/05	11.5*	45.2*	6.8*	0.2	—
	09/12/05–10/10/05	16.8*	–8.7*	8.5*	7.9*	—
	10/10/05–11/07/05	6.6*	–1.8	3.1	–6.5*	—
	11/07/05–12/05/05	–1.9	–8.9*	–4.8	–40.9*	—
	12/05/05–01/02/06	–7.9*	2.0	–4.4	—	—
	01/02/06–01/30/06	–8.9*	–18.9*	1.5	—	—

[z]Asterisks denote means significantly different from a rate of 0.0 $mg \cdot g^{-1} \cdot d^{-1}$ ($THSD_{0.05}$; n = 5).
AZ, *Rhododendron* 'Gibraltar'; ER, *R.* 'English Roseum; PMJ, *R.* 'P.J.M. Compact' (PJM).

accumulation was greater before November, roots still accumulated biomass during the winter (Table 1 and Table 2). A similar accumulation of root biomass in winter was also reported for *V. myrtillus* and *V. vitis-idaea* (Grelet et al., 2001). In PJM, because shoot biomass decreased during winter (Table 1), winter accumulation of root biomass may have been the result of increased storage of reserves in roots. Root N content also increased during winter in this cultivar (Table 3), whereas the C-to-N ratio remained relatively constant (Table 4).

By comparison, root biomass in ER and AZ decreased (Table 1) after a brief period of cold, dry weather in December (i.e., 5 d with minimum temperatures less than –6 °C) followed by warm, wet weather. This root loss resulted in ER and AZ losing 6% to 11% of their total N reserves (Fig. 1, Table 3) and a drop in root C-to-N ratio (Table 4). Temperature often plays a major role in root production (Ågren and Ingestad, 1987). The American Rhododendron Society lists cold hardiness for ER and PJM at –32 °C and for AZ at –26 °C. Assessments of cold hardiness are usually based on aboveground plant characteristics. However, cold hardiness of *Rhododendron* roots also differs among cultivars, ranging from –20 to –7 °C (Havis, 1976;

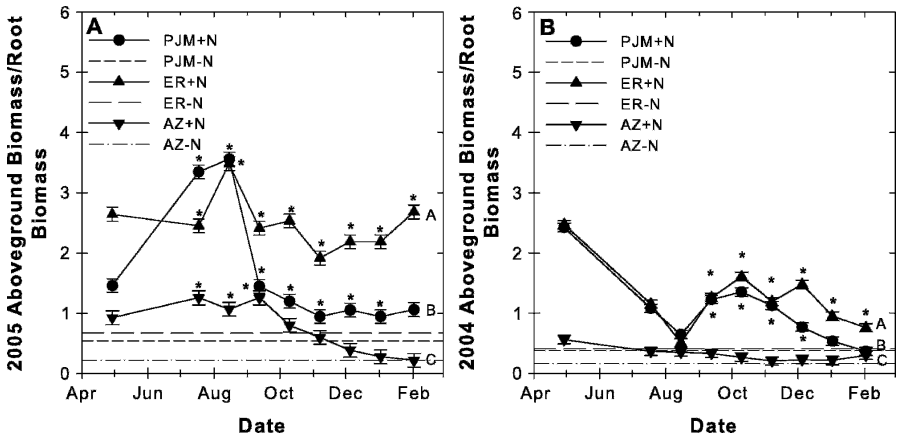

Fig. 3. Ratios of 2005 (**A**) and 2004 (**B**) aboveground to belowground biomass of *Rhododendron* 'P.J.M. Compact' (PJM), *R.* 'English Roseum' (ER), and *R.* 'Gibraltar' (AZ) grown in containers with (+N) or without (–N) additional nitrogen (N). Data points represent means; error bars represent SES (n = 5). Uppercase letters to the right of +N lines denote significant differences in response over time between cultivars (contrasts at $P < 0.05$). Year 2004 aboveground biomass is biomass of all aboveground 2-year-old structures. Year 2005 aboveground biomass is biomass of all aboveground 1-year-old structures. Average partitioning of plants in the –N treatment from Aug. 2005 through Feb. 2006 shown by horizontal lines (no significant change between dates). Asterisks beside +N data points (A, C, D, E) denote significant differences between +N and –N treatments within a date ($THSD_{0.05}$).

Studer et al., 1978). The root turnover that occurred in December may be a result of less cold hardiness in roots of ER and AZ compared with PJM. Cold hardiness of needles on conifers can be three to five times the level of roots (Coleman et al., 1992). If the decline in root biomass of ER and AZ were the result of low temperatures and root death, this would indicate that roots of these cultivars are sensitive at temperatures around –7 °C, which is four to five times warmer than aboveground cold hardiness temperatures. Increased concentrations of soluble sugar in conifer roots have been associated with increased cold hardening (Tinus et al., 2000). In our study, winter C-to-N ratios in roots remained constant in PJM, but dropped in ER and AZ (Table 4). Apparently, winter cryoprotection may be higher in PJM as a result of accumulation and maintenance of C-containing compounds in its roots.

Nitrogen uptake and storage. In +N plants, average N concentrations were the highest in July and then declined until November (Fig. 1). After November, average N concentrations remained relatively constant

Table 3. Nitrogen (N) concentration and content of roots, new (2005) stems and leaves, and old (2004) stems and leaves of *Rhododendron* 'P.J.M. Compact' (PJM), *R.* 'English Roseum' (ER), and *R.* 'Gibraltar' (AZ) grown in containers with additional nitrogen from Apr. 2005 to Feb. 2006.

		Concn ($mg \cdot g^{-1}$) or content (mg)									
		Roots		2005 Stems		2004 Stems		2005 Leaves		2004 Leaves	
Cultivar	Date	$mg \cdot g^{-1}$	mg	$mg \cdot g^{-1}$	mg	$mg \cdot g^{-1}$	mg	$mg \cdot g^{-1}$	mg	$mg \cdot g^{-1}$	mg
PJM	04/29/05	10.7	6.6	7.5	0.4	10.6	4.8	19.9	14.3	17.7	14.3
	07/18/05	9.8	17.6	10.6*	8.7	6.4	8.6	23.5*	114.8*	14.1*	7.6
	08/15/05	10.0*	41.5	8.4*	26.0*	6.2	12.0	18.7*	215.2*	13.3*	9.3
	09/12/05	10.1*	94.15*	9.2*	33.8*	6.6	42.7*	19.1*	187.5*	16.2*	74.4*
	10/10/05	8.9*	97.3*	8.6*	35.2*	6.6	69.1*	18.0*	168.5*	15.0*	70.9*
	11/07/05	8.1*	100.3*	8.9*	39.6*	6.9	78.5*	17.9*	159.9*	16.3*	80.4*
	12/05/05	6.6	117.0*	8.6*	45.5*	6.7	55.9*	17.4*	170.0*	16.4*	46.1*
	01/02/06	8.2*	126.2*	9.4*	44.4*	8.5*	46.7*	17.0	164.8*	16.8*	49.0*
	01/30/06	8.5*	141.2*	8.6*	39.7*	8.3*	46.2*	15.8	182.1*	—	—
ER	04/29/05	9.2	11.4	7.9	11.9	8.3	2.7	11.5*	15.9	10.4	17.4
	07/18/05	8.1*	32.8	8.6	15.7	4.8	8.4	19.8*	154.8*	12.7*	37.2
	08/15/05	7.4*	55.2	6.3*	34.1*	4.9	9.8	14.7*	291.4*	11.7*	21.2
	09/12/05	7.4*	87.7*	5.8*	39.8*	7.8	33.6*	13.9	298.0*	11.5*	91.4*
	10/10/05	6.3	81.9*	5.5*	41.1*	4.3	32.8*	11.3	317.2*	10.5*	158.4*
	11/07/05	5.4	110.4*	4.9*	54.7*	3.7	29.3*	10.7	295.1*	9.6	162.1*
	12/05/05	5.4	102.5*	4.8*	59.7*	3.6	34.0*	10.0	281.4*	9.8	178.7*
	01/02/06	5.1	94.6*	5.0*	55.9*	5.2	36.5*	10.6	307.5*	9.3	92.1*
	01/30/06	5.5	61.9*	4.4*	43.1*	5.7*	43.6*	9.4	323.5*	8.9	53.9*
AZ	04/29/05	10.9	10.5	7.1	0.8	9.9	5.0	22.4*	16.7	—	—
	07/18/05	11.9*	46.2	10.2*	9.5	9.5*	13.3	22.1*	81.5*	—	—
	08/15/05	10.7*	64.3*	9.4*	14.2	9.4*	20.4*	22.8*	105.7*	—	—
	09/12/05	9.5*	79.0*	7.4*	41.5*	9.2*	25.5*	21.5*	103.4*	—	—
	10/10/05	7.8*	106.2*	7.6*	33.3*	8.2*	29.3*	18.2*	114.3*	—	—
	11/07/05	6.6*	107.4*	8.2*	35.4*	9.3*	31.1*	15.0	79.3*	—	—
	12/05/05	8.8*	119.7*	9.4*	32.1*	10.3*	32.5*	12.5	22.6	—	—
	01/02/06	8.9*	118.4*	9.3*	33.7*	12.5*	35.9*	—	—	—	—
	01/30/06	9.9*	100.8*	10.6*	23.4*	12.4*	37.8*	—	—	—	—
Contrasts[y]											
PJM (time)		L, Q	L	Q	L, Q	Q	L, Q	L	L, Q	Q	L, Q
ER (time)		L	L, Q	L, Q	L, Q	Q	L	L, Q	L, Q	L, Q	L, Q
AZ (time)		Q	L, Q	Q	L, Q	L, Q	L	L, Q	Q	—	—
PJM vs. ER (time)		L, Q	L, Q	L, Q	L, Q	NS	L, Q	L, Q	L, Q	L, Q	L, Q
PJM vs. AZ (time)		L, Q	L, Q	NS	L, Q	L, Q	L, Q	L, Q	L, Q	—	—
ER vs. AZ (time)		L, Q	L, Q	L, Q	L, Q	L, Q	NS	L, Q	L, Q	—	—

[z]Asterisks denote significant differences between treatments with and without nitrogen within a date ($THSD_{0.05}$; n = 5).
[y]Significant ($P < 0.05$) polynomial responses of variables over time for each cultivar and between cultivars.
AZ, *Rhododendron* 'Gibraltar'; ER, *R.* 'English Roseum; L, linear; PMJ, *R.* 'P.J.M. Compact' (PJM); Q, quadratic.
[NS]Nonsignificant.

Table 4. Ratio of carbon to nitrogen (CN) of roots, new (2005) stems and leaves, and old (2004) stems and leaves of *Rhododendron* 'P.J.M. Compact' (PJM), *R.* 'English Roseum' (ER), and *R.* 'Gibraltar' (AZ) grown in containers with additional nitrogen from Apr. 2005 to Feb. 2006.

		CN ratio				
Cultivar	Date	Roots	2005 Stems	2004 Stems	2005 Leaves	2004 Leaves
PJM	04/29/05	12.5a[z]	62.8a	44.3a	23.2a	28.3a
	07/18/05	76.9a	43.7a	74.3b	20.8a	33.0a
	08/15/05	142.7b	55.2a	77.0b	25.8a	34.4a
	09/12/05	195.2b	51.5a	71.9b	24.7a	29.0a
	10/10/05	234.1b	55.9a	72.2a	27.3a	31.9a
	11/07/05	281.9b	54.2a	70.0a	27.3a	29.7a
	12/05/05	297.2b	55.6a	72.6b	28.1a	28.4a
	01/02/06	286.8b	50.9a	57.5a	28.5a	28.8a
	01/30/06	297.2b	55.9b	57.4b	30.7a	—
ER	04/29/05	22.5a	57.3a	56.9a	41.5b	48.4b
	07/18/05	143.7b	51.9a	96.9b	23.8a	37.5b
	08/15/05	255.2c	72.1b	95.3b	31.9b	49.7b
	09/12/05	352.0c	75.8b	98.6c	24.1b	40.9b
	10/10/05	486.6c	85.8b	107.9b	41.8b	44.4b
	11/07/05	561.1c	94.6b	128.9b	44.5b	48.7b
	12/05/05	527.5c	97.5b	130.7c	48.2c	48.1b
	01/02/06	495.5c	93.3b	98.2b	45.2b	48.5b
	01/30/06	485.8c	106.2c	82.6c	51.4b	52.8b
AZ	04/29/05	14.2a	64.6a	46.9a	20.8a	—
	07/18/05	56.9a	44.9a	78.8a	20.7a	—
	08/15/05	85.9a	49.0a	79.6a	20.3a	—
	09/12/05	117.8a	61.9a	50.8a	21.6a	—
	10/10/05	158.9a	62.4a	56.6a	25.5a	—
	11/07/05	169.5a	56.9a	50.3a	30.4a	—
	12/05/05	106.5a	49.3a	45.1a	36.9b	—
	01/02/06	96.8a	49.5a	37.1a	—	—
	01/30/06	74.7a	44.2a	37.5a	—	—
Contrasts[y]						
PJM (time)		L, Q	NS	NS	L	NS
ER (time)		L, Q	L, Q	L, Q	L, Q	L, Q
AZ (time)		L, Q	L, Q	NS	L, Q	—
PJM vs. ER (time)		L, Q	L, Q	L, Q	L, Q	L, Q
PJM vs. AZ (time)		L, Q	L, Q	NS	L, Q	—
ER vs. AZ (time)		L, Q	L, Q	L, Q	L, Q	—

[z]Means within a column and date followed by the same letter are nonsignificant ($THSD_{0.05}$; n = 5).
[y]Significant ($P < 0.05$) polynomial responses of variables over time for each cultivar and between cultivars. AZ, *Rhododendron* 'Gibraltar'; CN, ratio of carbon to nitrogen; ER, *R.* 'English Roseum; L, linear; PMJ, *R.* 'P.J.M. Compact' (PJM); Q, quadratic.
[NS]Nonsignificant.

in ER and PJM, and increased in AZ. Declining N concentrations from July to November were the result of changes in the roots, new stems, and new leaves (Table 3). In ER, declining N concentrations were also the result of decreasing N concentrations in old leaves. Lower N concentrations were associated with increased biomass (therefore nutrient dilution), indicating that N availability to +N plants was not restricting growth. Others reported concentrations similar to those in the current study in deciduous and evergreen *Rhododendron* cultivars (Clark et al., 2003). Changes in N concentration after November were related to N reallocation and not growth. For example, in +N plants, N was reallocated from new leaves to roots and old stems in PJM, from new stems and leaves to old stems in ER, and from senescing leaves to roots and stems in AZ (Fig. 1, Table 3). A similar uncoupling of growth and N translocation in autumn and winter has also been described for *Calluna* (Andersen and Michelsen, 2005).

The pattern of total N accumulation in +N plants differed among cultivars, with N uptake occurring from May to October in AZ and ER, and from May to November in PJM (Figs. 1 and 2). Between 13% to 18% of maximum N content accumulated after N applications stopped. In contrast, plants in the –N treatment contained the most N in October and accumulated 37 to 67 mg N from substrate, irrigation water, and fertilizer in the original liner. Using ^{15}N ammonium nitrate, Grelet et al. (2001) determined that N uptake by *V. myrtillus* and *V. vitis-idaea* occurred as late as November, and uptake between September and November accounted for ≈25% of total plant uptake. Andersen and Michelsen (2005) reported that N uptake occurred after November in *Calluna*, even when soil temperatures were ≈0 °C. We did not detect any N uptake after November in our study, but N availability in the growing substrate may have been too low to cause detectable changes in total plant N content.

We estimated that maximum N uptake by +N plants was 2 to 5 $mg \cdot d^{-1}$ depending on the cultivar (Fig. 2). These rates are similar to those reported for container-grown deciduous and evergreen *Rhododendron* cultivars reported by others (Evans and Dodge, 2002; Ristvey et al., 2001). From October to December, +N plants of the deciduous cultivar lost 31% of their maximum N (Fig. 1) to leaf senescence (Tables 1 and 3), and after December plants lost another 17% of their maximum N to decreased biomass and concentrations in roots (8%) and new stems (9%). By comparison, after December, ER plants lost 20% of their maximum N to decreased biomass of roots (6%) and new stems (3%), and to decreased biomass and N concentration in old leaves (11%), and PJM plants lost 14% of their maximum N to decreased biomass in old stems (7%) and leaves (7%). In each cultivar, N concentrations decreased during winter, indicating that although N resorption from senescing leaves may have occurred, N losses from root turnover and maintenance functions can cause substantial decreases in N reserves during the winter.

Seasonal changes in nitrogen demand between structures. Understanding when different plant structures are N sinks may be helpful to determine how N limitations during the year impact growth, N storage, and, ultimately, plant quality. For example, N import for the evergreen cultivars (PJM and ER) was greatest for new leaves in July (3.6–4.9 $mg \cdot d^{-1}$), for new stems in August (0.6–0.7 $mg \cdot d^{-1}$), and for old leaves (2.3–2.5 $mg \cdot d^{-1}$), old stems (0.9–1.1 $mg \cdot d^{-1}$), and roots (1.2–1.9 $mg \cdot d^{-1}$) in September. Thus, for the evergreen cultivars in this study, N limitations had the most impact on new growth in midsummer and on older structures and roots in autumn. Nitrogen uptake by the evergreen cultivars was also positively correlated with N import to roots (PJM, $R = 0.741$; ER, $R = 0.763$), new stems (PJM, $R = 0.603$; ER, $R = 0.654$), and old leaves (PJM, $R = 0.639$; ER, $R = 0.691$), indicating that N availability after May had the most impact on the N dynamics of these structures. In comparison, N import by the deciduous cultivar (AZ) was greatest to old stems in August (0.25 $mg \cdot d^{-1}$), new stems in September (0.98 $mg \cdot d^{-1}$), and roots in October (0.97 $mg \cdot d^{-1}$), and N import to new leaves after May was less than 0.81 $mg \cdot d^{-1}$. In AZ, N limitations in summer had little impact on leaf growth, and both old and new stems, as well as roots, became N sinks in autumn.

The pattern of N demand (for use and storage) by various structures on +N plants varied among cultivars ($P < 0.05$; Fig. 4). Nitrogen demand by roots and stems, for example, increased from May to February and was higher in the deciduous cultivar than in the evergreen cultivars ($P < 0.05$). Nitrogen demand by stems accounted for up to 40% of total N uptake in AZ and less than 22% in ER and PJM, whereas N demand by roots accounted for less than 20% of total N uptake in ER and 40% to 60% in PJM and AZ. Nitrogen demand by new leaves in PJM decreased from August to November in conjunction with large increases in N demand by roots and old leaves, followed by large increases in N demand by old stems. In old leaves, on the other hand, N demand

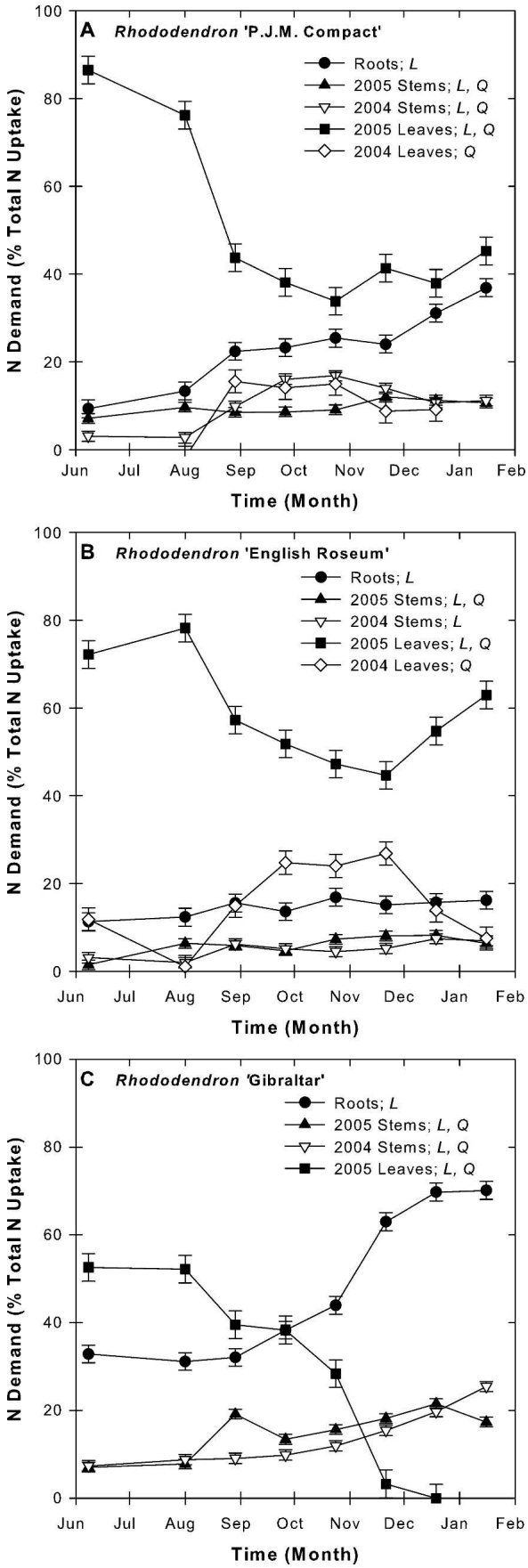

Fig. 4. Nitrogen (N) demand of roots, new (2005) stems and leaves, and old (2004) stems and leaves of three *Rhododendron* cultivars grown in containers with additional N from Apr. 2005 to Feb. 2006. Data points represent means; error bars represent SES (n = 5). The *L* and *Q* in legends after a response variable represent significant ($P < 0.05$) linear (*L*) and quadratic (*Q*) contrasts over time.

decreased from November to February in conjunction with large increases by roots and new leaves. By comparison, N demand of new leaves in ER decreased from August to December in conjunction with large increases by old leaves, and N demand by old leaves decreased from December to February in conjunction with large increases in new leaves. New and old leaves of evergreen *Rhododendron* appear to play a dynamic role in N storage during winter when reserves are moved between leaves and other structures, possibly in response to environmental conditions. This movement of N between different structures in the winter may be used for maintenance of the photosynthetic apparatus in the evergreen plants (Karlsson, 1994a).

The evergreen cultivars stored most N in new leaves whereas the deciduous cultivar stored the most in the roots. Roots, however, were also a major location for N storage in PJM. The locations for N storage in AZ and PJM are similar to those found by Bi et al. (unpublished data). They estimated that a deciduous *Rhododendron* cultivar, *R.* 'Cannon's Double', stored 50% to 65% of its total N in roots, 10% to 15% in old stems, and 20% to 40% in new stems, whereas an evergreen cultivar, *R.* 'P.J.M. H-1', stored 40% to 50% of its total N in leaves, ≈30% in roots, and the remainder in stems. Storage of N in roots and stems is common in deciduous woody plants (Millard, 1996). Ristvey et al. (2001) found that leaves of evergreen azalea contained ≈50% of total plant N, similar to the amount measured in ER leaves, but more than the amount in PJM leaves.

Evergreen plants have been reported to use various methods for storing N depending on leaf phenology and developmental stage (Karlsson, 1994a, b) and N source (Clark et al., 2003). In evergreen *R. ferrugineum*, N is stored over winter in older leaves and then remobilized for new growth throughout the following growing season (Lamaze et al., 2003; Pasche et al., 2002b). Old needles on conifer seedlings also contribute a high proportion of N to new growth (Nambiar and Fife, 1987). Nitrogen storage differences between the two evergreen cultivars in our study primarily occurred in roots and leaves. During winter, PJM stored more N in roots than ER, whereas ER stored more N in leaves. These different N storage locations in evergreen cultivars may account for reported species differences in the dependence of evergreen plants on remobilization of N from overwintering structures (Jonasson, 1989; Lamaze et al., 2003). For many evergreen species, leaf N resorption and abscission occur synchronously with stem growth (Jonasson, 1989; Pornon et al., 1998). This appeared to be the case in ER, where little to no leaf abscission occurred during the study; however, leaf abscission began in winter in PJM. Differences in N storage between these cultivars may be a result of differences in leaf retention and phenology similar to that described for different-age plants of *R. ferrugineum* (Pasche et al., 2002a).

Nitrogen uptake efficiency. Nitrogen uptake continued up to 2 months after N applications ceased in early September (Fig. 1 and Fig. 2). This autumn uptake made a significant contribution to the total plant N, accounting for 13% to 16% of total uptake between May and February. Late-season uptake may play an important role in supplementing N reserves required for next season's growth and for balancing N losses from leaf abscission, root turnover, and winter maintenance. Tagliavini et al. (1999) suggested that N uptake in autumn may contribute up to 70% more to N storage in deciduous plants than uptake in spring. Although N uptake by container-grown *Rhododendron* occurred in autumn, N uptake efficiency peaked in November in the evergreen cultivars, but declined between June and February in the deciduous cultivar (Fig. 5). These results indicate that N applications to transplanted liners should include fertilizer with low N availability after transplanting, followed by high N availability in mid to late summer. Fertilizer application in autumn is not a common practice for container-grown nursery plants because of an increased potential for problems with winter hardiness (Alt, 1998; Bi et al., 2004; Rikala et al., 2004). However, autumn applications of foliar fertilizers are often used in tree fruit nurseries (Bi et al., 2004; Sanchez et al., 1990). We have also found (unpublished data) that foliar urea applications in autumn to container-grown *Rhododendron* increased N reserves by 40% to 60%, and improved growth the following season. Autumn foliar urea applications may be a useful method to increase N reserves in *Rhododendron*, especially when available N is low in the growing substrate.

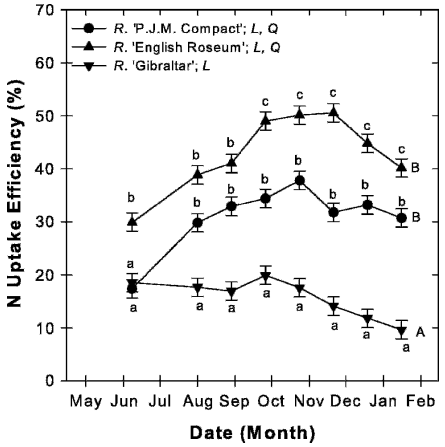

Fig. 5. Nitrogen (N) uptake efficiency of three *Rhododendron* cultivars grown in containers with additional N from May 2005 through Feb. 2006. Data points represent means; error bars represent SES (n = 5). Data points within a date denoted by the same lowercase letter are not significantly different ($THSD_{0.05}$). Lines denoted by the same uppercase letter indicate similar responses between cultivars over time (polynomial contrasts at $P > 0.05$). *L,* linear; *Q,* quadratic.

Our results also indicate that optimal fertilizer strategies may differ between evergreen and deciduous cultivars as a result of differences in N uptake efficiency (Fig. 5). Extended leaf longevity has been explained both as an adaptation to conserve nutrients in low-nutrient environments and to increase the seasonal window for C gain (Chabot and Hicks, 1982; Jonasson, 1989; Reich et al., 1992; Small, 1972). Evergreen species are also reported to resorb a higher percentage of leaf nutrients before leaf abscission than deciduous species (Small, 1972). A high nutrient resorption, in combination with the prolonged life span, yields a long residence time for nutrients within the evergreen plants. As a consequence, evergreen plants assimilate more C per unit of invested nutrients than the deciduous species. These observations help explain why the evergreen cultivars in our study continued to accumulate biomass into early winter (Fig. 1), and why biomass accumulation only stopped when environmental conditions were probably limiting to photosynthesis (Harris et al., 2005). This indicates that the leaves on evergreen *Rhododendron* not only act as a location for N storage, but also the retention time of leaves across growing seasons may help to prolong the photosynthetic period. Our observations that the C-to-N ratios in storage tissues of the evergreen *Rhododendron* cultivars increased during the winter (Table 4) also support this hypothesis. These differences in nutrient and C dynamics between evergreen and deciduous *Rhododendron* have important implications to nutrient management strategies for container-grown plants.

Literature Cited

Ågren, G.I. and T. Ingestad. 1987. Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. Plant Cell Environ. 10:579–586.

Alt, D. 1998. N-fertilization of nursery crops in the field: A review, part 1. Gartenbauwissenschaft 63:165–170.

Alt, D., H. Hinrichs, and H. Kohstall. 1994. Influence of increasing amounts of nitrogen on rhododendron. Acta Hort. 364:89–94.

Andersen, L. and N.S. Bentsen. 2003. Survival and growth of *Abies nordmanniana* in forest and field in relation to stock type and root pruning prior to transplanting. Ann. Sci. 60:757–762.

Andersen, L.C. and A. Michelsen. 2005. Off-season uptake of nitrogen in temperate heath vegetation. Oecologia 144:585–597.

Azam, F., F.J. Stevenson, and R.L. Mulvaney. 1989. Chemical extraction of newly immobilized 15N and native soil N as influenced by substrate addition rate and soil treatments. Soil Biol. Biochem. 21:715–722.

Bi, G., C.F. Scagel, L. Cheng, S. Dong, and L.H. Fuchigami. 2004. Spring growth of almond nursery trees depends upon both nitrogen reserves and spring nitrogen application. J. Hort. Sci. Biotechnol. 78:853–858.

Bi, G., C.F. Scagel, L.H. Fuchigami, and R.P. Regan. 2006. Differences in growth, nitrogen uptake, and storage between two container-grown *Rhododendron* cultivars. J. Environ. Hort. 25:13–20.

Bloom, A.J., F.S. Chapin, III, and H.A. Mooney. 1985. Resource limitation in plants: An economic analogy. Ann. Rev. Ecol. Systematics 16:363–393.

Broschat, T.K. 2005. Rates of ammonium-nitrogen, nitrate-nitrogen, phosphorus, and potassium from two controlled-release fertilizers under different substrate environments. HortTechnology 15:332–335.

Cabrera, R.I. 1997. Comparative evaluation of nitrogen release patterns from controlled-release fertilizer by nitrogen leaching analysis. HortScience 34:669–673.

Chabot, B.F. and D.J. Hicks. 1982. The ecology of leaf life spans. Ann. Rev. Ecol. System. 13:229–259.

Chapin, F.S., III and K. van Cleve. 1991. Approaches to studying nutrient uptake, use and loss in plants, p. 185–207. In: R.W. Pearcy, J. Ehleringer, H.A. Mooney, and P.W. Rundel (eds.). Plant physiological ecology. Field methods and instrumentation. Chapman and Hall, New York.

Clark, M.B., H.A. Mills, C.D. Robacker, and J.G. Latimer. 2003. Influence of nitrate: Ammonium ratios on growth and elemental concentration in two azalea cultivars. J. Plant Nutr. 26:2503–2520.

Coleman, M.D., T.M. Hinckley, G. McNaughton, and B.A. Smit. 1992. Root cold hardiness and native distribution of subalpine conifers. Can. J. For. Res. 22:932–938.

Evans, R.E. and L. Dodge. 2002. Nitrogen and water use of container-grown woody ornamentals. California Ornamental Res. Federation News 6:3–11.

Grelet, G., I.J. Alexander, and M.F. Proe. 2001. Leaf habit influences nitrogen remobilization in *Vaccinium* species. J. Expt. Bot. 52:993–1002.

Grelet, G.A., I. Alexander, P. Millard, and M. Proe. 2003. Does morphology or the size of the internal nitrogen store determine how *Vaccinium* spp. responds to spring nitrogen supply? Funct. Ecol. 17:690–699.

Harris, G.C., V. Antoine, M. Chan, D. Nevidomskyte, and M. Koniger. 2005. Seasonal changes in photosynthesis, protein composition and mineral content in *Rhododendron* leaves. Plant Sci. 170:314–325.

Harris, J.R., N. Bassuk, R. Zobel, and T. Whitlow. 1995. Root and shoot growth periodicity of Green Ash, Scarlet Oak, Turkish Hazelnut, and Tree Lilac. J. Amer. Soc. Hort. Sci. 120:211–216.

Havis, J.R. 1976. Root hardiness of woody ornamentals. HortScience 11:385–399.

Hoffman, W.A. and H. Poorter. 2002. Avoiding bias in calculations of relative growth rate. Ann. Bot. (Lond.) 90:37–42.

Huett, D.O. and B.J. Gogel. 2000. Longevities and nitrogen, phosphorus, and potassium release patterns of polymer-coated controlled-release fertilizer at 30°C and 40°C. Commun. Soil Sci. Plant Anal. 31:959–973.

Jonasson, S. 1989. Implications of leaf longevity, leaf nutrient re-absorption and translocation for the resource economy of five evergreen plant species. Oikos 56:121–131.

Jonasson, S. 1995. Resource allocation in relation to leaf retention time of the wintergreen *Rhododendron lapponicum.*. Ecology 76:475–485.

Karlsson, P.S. 1994a. Photosynthetic capacity and photosynthetic nutrient-use efficiency of *Rhododendron lapponicum* leaves as related to leaf nutrient status, leaf age and branch reproductive status. Funct. Ecol. 8:694–700.

Karlsson, P.S. 1994b. The significance of internal nutrient cycling in branches for growth and

reproduction of *Rhododendron lapponicum.* Oikos 70:191–200.
Kolb, K.J. and R.D. Evans. 2002. Implications of leaf nitrogen recycling on the nitrogen isotope composition of deciduous plant tissues. New Phytol. 156:57–64.
Lamaze, T., F. Pashe, and A. Pornon. 2003. Uncoupling nitrogen requirements for spring growth from root uptake in a young evergreen shrub (*Rhododendron ferrugineum*). New Phytol. 159:637–644.
Marschner, H. 1995. Mineral nutrition of higher plants. 2nd ed. Academic Press, San Diego, CA.
Merhaut, D.J., E.K. Blythe, J.P. Newman, and J.P. Albano. 2006. Nutrient release from controlled-release fertilizer in acid substrate in a greenhouse environment: I. Leachate electrical conductivity, pH, and nitrogen, phosphorus, and potassium concentrations. HortScience 41:780–787.
Mertens, W.C. and R.D. Wright. 1978. Root and shoot growth rate relationships of two cultivars on Japanese holly. J. Amer. Soc. Hort. Sci. 103:722–724.
Milla, R., P. Castro-Diez, M. Maestro-Marinez, and G. Montserrat-Marti. 2005. Relationships between phenology and the remobilization of nitrogen, phosphorus, and potassium in branches of eight Mediterranean evergreens. New Phytol. 168:167–178.
Millard, P. 1996. Ecophytology of the internal cycling of nitrogen for tree growth. J. Plant Nutr. Soil Sci. 159:1–10.
Nambiar, E.K.S. and D.N. Fife. 1987. Growth and nutrient retranslocation in needles of radiate pine in relation to nitrogen supply. Ann. Bot. (Lond.) 60:147–156.
Pasche, R., A. Pornon, and T. Lamaze. 2002a. Do mature leaves provide a net source of nitrogen supporting shoot growth in *Rhododendron ferrugineum?* New Phytol. 154:99–105.
Pasche, F., A. Pornon, and T. Lamaze. 2002b. Source–sink nitrogen relationships between the different leaf generations and the growing shoots in the evergreen shrub *Rhododendron ferrugineum* L.: A 15N study. New Phytol. 154:99–105.
Pornon, A., B. Doche, and N. Escavarage. 1998. Cycle interne de l'azote dans une nanophanérophyte subalpine (*Rhododendron ferrugineum*) se développant sur sols pauvres. Ecologie 29:403–406.
Proe, M.F., A.J. Midwood, and J. Graig. 2000. Use of stable isotopes to quantify nitrogen, potassium, and magnesium dynamics in your Scotts pine (*Pinus sylvestris*). New Phytol. 146: 461–469.
Reich, P.B., M.B. Walters, and D.S. Ellsworth. 1992. Leaf life span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol. Monogr. 62:365–393.
Rikala, R., J. Heiskanen, and M. Lahti. 2004. Autumn fertilization in the nursery affects growth of *Picea abies* container seedlings after transplanting. Scand. J. For. Res. 18: 409–414.
Ristvey, A.G., J.D. Lea-Cox, and D.S. Ross. 2001. Nitrogen uptake, partitioning, and loss in container-production systems. Proc. Southern Nurserymens Assoc. Res. Conference 46:87.
Sanchez, E.E., T.L. Righetti, D. Sugar, and P.B. Lomard. 1990. Seasonal differences, soil texture and uptake of newly absorbed nitrogen in field-grown pear trees. J. Hort. Sci. 65: 395–400.
Sandrock, D.R., A.N. Azarenko, and T.L. Righetti. 2005a. Fertilization of two container-grown woody ornamentals based on their specific nitrogen accumulation patterns. HortScience 40:451–456.
Sandrock, D.R., T.L. Righetti, and A.N. Azarenko. 2005b. Isotopic and nonisotopic estimation of nitrogen uptake efficiency in container-grown woody ornamentals. HortScience 40: 665–669.
Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Can. J. Bot. 50: 2227–2233.
Studer, E.J., P.L. Steponkus, G.L. Good, and S.C. Wiest. 1978. Root hardiness of container grown ornamentals. HortScience 13:172–174.
Tagliavini, M., P. Millard, M. Quartieri, and B. Marangoni. 1999. Timing of nitrogen uptake affects winter storage and spring remobilization of nitrogen in nectarine *Prunus persica* var. *nectarine* trees. Plant Soil 211:149–153.
Tinus, R.W., K.E. Burr, N. Atzmon, and J. Riov. 2000. Relationship between carbohydrate concentration and root growth potential in coniferous seedling from three climates during cold hardening and dehardening. Tree Physiol. 20:1097–1104.
van den Driessche, R. 1991. Influence of container nursery regimes on drought resistance of seedlings following planting. I. Survival and growth. Can. J. For. Res. 21:555–565.
Walters, D.T. and G.L. Malzer. 1990. Nitrogen management and nitrification inhibitor effect on nitrogen-15 urea: I. Yield and fertilizer use efficiency. Soil Sci. Soc. Amer. J. 54: 115–122.
Witt, H.H. 1994. Regulation of nitrogen supply of *Rhododendron* hybrids. Acta Hort. 364: 79–87.